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TAXONOMY OF PSATHYROTES (COMPOSITAE: SENECIONEAE)

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Psathyrotes comprises five species of humble herbs, two in the Chihuahuan Desert and three in the Sonoran Desert and southwestern Great Basin. They typically grow in dry, sandy washes, among sand dunes, or on gravelly benches and alluvial fans. Economically these plants are are of no known consequence; aesthetically they are not particularly appealing. They have received little attention from botanists other than compilers of regional floras and, therefore, have been relatively poorly known. Heretofore, morphological circumscriptions of at least two species and geographic ranges of three have been confusedly or inaccurately delineated in regional and local floras. We hope that our observations will serve to abrogate the confusion and to redress the inaccuracies.

A brief chronology of the taxonomic history of the genus follows:

1848. Nuttall described the first plant to be assigned to the genus, *Bulbostylis annua,* placing it in a monotypic section, *Psathyrotus* [sic]. (*Bulbostylis* DC. is now generally considered to be a synonym of *Brickellia* Ell., a member of Eupatorieae.) Later in the same year, Torrey named a new species, *Tetradymia ramosissima,* placing it in a new, monotypic subg. *Polydemia*. (*Tetradymia* is a member of Senecioneae.)

1853. Gray altered the rank of Nuttall's section to genus, corrected the orthography to *Psathyrotes,* and added a second species (*P. scaposa*), indicating that the genus should be "provisionally referred, I think, to Senecionideae of the subtribe Senecioneae". He did not mention *Tetradymia ramosissima.*

1854. Gray described *Psathyrotes incisa* as a third species of the genus. At the same time, Gray said that Torrey had informed him that *Tetradymia ramosissima* and *P. annua* refer to the same species and asserted that Torrey "had rightly indicated the affinities of the plant" (i.e., with *Tetradymia*).

1859. Gray (Bot. Mex. Bound.) transferred *P. incisa* to a new, monotypic genus, *Trichoptilium,* in Helenieae, commenting that Torrey had "pointed out the oversight I [Gray] had committed in respect to the pappus, and which led me wrongly to refer the plant to Psathyrotes".

1868. Without compromising Torrey, Gray acknowledged that he (Gray) "had confounded" *P. annua* with "a related but distinct species", *Tetradymia ramosissima,* which he transferred to *Psathyrotes.* He treated these two species as belonging to one section and *P. scaposa* as belonging to a second. Both sections were carefully diagnosed but neither was formally named.

1873. Bentham (in *Genera plantarum*) listed *Trichoptilium* and *Psathyrotes* at the end of Helenieae, remarking that, while the pappus of *Psathyrotes* is close to that of Senecioneae, other characters seem to indicate affinity with Helenieae. He also indicated that whether the pappus of *Trichoptilium* is interpreted as bristles or fimbriate paleae, it is nevertheless similar to that of *Psathyrotes* (see also Bentham, 1873, p. 449).

1874. Gray, partly in response to Bentham, stated that *Psathyrotes* belongs in Senecioneae close to *Luina* Benth. and *Tetradymia.* He indicated that *Trichoptilium* might also belong in Senecioneae. Additionally, he transferred *Peucephyllum* A. Gray (a monotype, *P. schottii,* originally referred to Eupatorieae by Gray but included in Senecioneae next to *Luina* by Bentham) to *Psathyrotes* as a distinct section.

1880. Gray briefly characterized a new species, *P. pilifera,* and indicated its close affinity to *P. annua* and *P. ramosissima.*

1884. In the *Synoptical flora,* Gray maintained *Psathyrotes* in Senecioneae, referring *P. annua, P. pilifera,* and *P. ramosissima* to one section and *P. scaposa* to a second (both still nameless). He returned *P. schottii* to *Peucephyllum* without comment.

1889. In his treatment for Compositae for *Die natürlichen Pflanzenfamilien,* Hoffmann referred *Psathyrotes* (with four species) to Senecioneae without comment.

1911. Brandegee described *P. purpusii,* stating that it "is a very distinct species" and "perhaps it should be considered the type of a genus".

1927. Rydberg, in the last comprehensive treatment of these plants (in N. Amer. Fl.), segregated Brandegee's species to a monotype,

Psathyrotopsis, wrongly stating that the tube of the corolla equals the throat. He also segregated *P. scaposa* to a monotype, *Pseudobartlettia.* The other species *(P. annua, P. pilifera,* and *P. ramosissima)* were retained in *Psathyrotes.* These three "genera" were grouped together in his subtribe "Senecionanae". He placed *Peucephyllum* in his subtribe "Luinanae", commenting that it "is an abnormal genus" in Senecioneae "and probably should be transferred to Astereae, next to *Ericameria*".

Generic Relationships

Cronquist (1955), Powell and Turner (1974), and others have remarked the heterogeneity and artificiality of Helenieae and have suggested that most genera historically assigned to this dust bin of a tribe would be better placed in Heliantheae or Senecioneae. In particular, Cronquist (1960) said, *"Psathyrotes, Peucephyllum* and some other small southwestern genera have customarily been excluded from Heliantheae (Helenieae) because of their capillary pappus, and referred to the Senecioneae instead. Their relationship to the main bulk of the Senecioneae is doubtful, however, and further investigation of the affinities of these genera is well warranted." Actually, among *Psathyrotes* only *P. pilifera* has a truly capillary pappus (in other species the bristles are rather coarse) and in southernmost colonies of *Peucephyllum* the pappus consists of well developed squamellae subtended by coarse bristles. Cronquist (1955) suggested the "origin of a capillary pappus by longitudinal fission of the scales" and proposed that steps in such a development are illustrated by several genera including *Dyssodia.* Strother (1969) indicated, however, that the simple squamellate pappus in *Dyssodia* is a derived condition and that the primitive pappus in the genus consists of squamellae formed of basally coalesced bristles.

In spite of these contradictory interpretations of pappus, there seems little doubt that *Psathyrotes* and *Peucephyllum* are closely related. The two are very similar in details of corollas, style branches, anthers, and achenes. The branching pattern of robust, suffrutescent plants of *P. ramosissima* is quite like that of *Peucephyllum,* although the latter is decidedly shrubby and has distinctive foliage. Carlquist (1962) included *Peucephyllum* in his survey of wood anatomy in Senecioneae and concluded that the wood is highly specialized but affords no character expressions suggesting a particular taxonomic placement. In their survey of pollen ultrastructure in Compositae, Skvarla and Turner (1966) assigned pollen of *Psathyrotes annua* to their Helianthoid-type and pollen of *Peucephyllum* to their Senecioid-type. Meiotic chromosome morphology and chromosome numbers are similar in *Psathyrotes* ($x = 19, 17$) and *Peucephyllum* ($x = 20$). Collectively, these data encourage recognition of separate but closely related genera.

Historically, as outlined above, these genera have been associated with *Trichoptilium* A. Gray, *Tetradymia* DC., and *Luina* Benth. The similarity between *Psathyrotes* and *Trichoptilium* ($x = 13$) is wholly

superficial; the relationship between them is remote. *Trichoptilium* is probably best placed in Eriophyllinae. *Tetradymia* ($x = 30$), *Luina* ($x = 30$) and a few other genera form a distinct alliance within Senecioneae (Strother, 1974) but are not closely related to *Psathyrotes* and *Peucephyllum*.

Where, then, did *Psathyrotes* come from? We still don't know. Careful postulation of an archetype combining putatively primitive character states for members of the genus allows development of a reasonable answer. Despite warnings of possible typological entrapment (Davis and Heywood, 1963), this seems an acceptable approach for determining affinities in many groups of Compositae, since several trends of specialization within the family are fairly well documented (Cronquist, 1955).

An archetype for *Psathyrotes* would have been a perennial, perhaps suffrutescent, herb with alternate, laminar, probably woolly, leaves, a simple capitulescence, a 2–3-seriate involucre of scarcely differentiated phyllaries, many (ca 50?) florets in each head, disc corollas with short tubes and lobes and relatively long, cylindrical throats, sagittate anthers, weakly appendaged, papillate style branches, and pyramidal achenes supporting a coarsely setose, 2–4-seriate pappus. Using this hypothetical but reasonable characterization of an ancestor for *Psathyrotes* as a basis for comparison, several aspects of morphology (e.g., habit, indument, involucre, corollas, style branches, and anthers) suggest *Hulsea* Torr. & Gray as a possible relative. *Hulsea* comprises about ten species of perennial or annual herbs that grow at middle to high elevations in western North America, especially in the drier mountains of the southwestern Great Basin and northwestern Sonoran Desert. Skvarla and Turner (1966) assigned pollen of *Hulsea carnosa* Rydb. to their Helianthoid-type. Cytological evidence supports morphological arguments for propinquity, since the chromosome base number of *Hulsea* ($x = 19$) is the same as that of primitive species of *Psathyrotes* (see below). Members of both genera are strongly scented with balsamic or turpentine odors, perhaps reflecting underlying chemical similarities.

Traditionally, *Hulsea* has been assigned to Helenieae. In 1962, Turner suggested a possible alliance to Senecioneae. Ornduff et al. (1967) agreed and indicated that both *Hulsea* and *Whitneya* ($n = 38$) belong in Senecioneae near *Arnica* ($x = 19$). Powell and Turner (1974) recently presented arguments for transferring several genera (Perityllinae, including *Hulsea*) from Helenieae to Senecioneae. They said that *Hulsea* might be "viewed as a possible ancestral prototype" for Perityllinae. While derivation of *Psathyrotes* and *Peucephyllum* from extant members of *Hulsea* seems unlikely, an hypothesis that these three genera derived from a fairly immediate common ancestor does seem reasonable. We do not feel, however, that *Psathyrotes* or *Peucephyllum* should be added to Perityllinae sensu Powell and Turner but rather that they belong to a separate, related group for which we are not yet prepared to offer a circumscription.

Chromosomes and Species Relationships

We have studied chromosomes in four species of *Psathyrotes* and chromosome numbers are now known for all five species of the genus (Table 1). Our observations were made from standard aceto-carmine

Table 1. Chromosome Counts for Psathyrotes. Pilz and Strother are abbreviated *P* and *S*, respectively, in citing collections; our vouchers are in UC. Our counts are reported as meiotic pairing configurations at diakinesis or early first metaphase. Parenthetical numbers refer to numbers of individuals examined.

Psathyrotes annua (Nutt.) A. Gray

CA, Inyo Co., ca 15 mi E Keeler, *P 1223,* **17 II**; 4 mi N Darwin, *Kyhos 58–196* (JEPS), **17 II** (reported as *P. ramosissima,* Ornduff et al., 1963).

CA, Kern Co., Red Rock Canyon, *Hill 47871–G* (DS), **17/17** at first anaphase (unpublished).

NV, Clark Co., 3 mi E Indian Springs, *P 1185,* **17 II.**

NV, Esmeralda Co., 22 mi W Tonopah, *P 858,* **17 II**; 7 mi S Goldfield, *Spellenberg 2107* (NY), **17 II** (Spellenberg, 1971a; 1971b).

NV, Lincoln Co., 12 mi S Alamo, *P 813,* **17 II**; 4 mi W Crystal Springs, *P 817,* **17 II.**

NV, Mineral Co., near Basalt, *P 854,* **17 II.**

NV, Nye Co., 16 mi W Lockes, *P 859,* **17 II plus 1—3 B.**

NV, Pershing Co., 15 mi S Lovelock, *P 729,* **17 II.**

NV, Washoe Co., 12 mi NW Nixon, *P 738* and *739,* **17 II**; W edge Winnemucca Dry Lake, *Ornduff 4202* (UC), **17 II** (Ornduff et al., 1963).

UT, Washington Co., 4 mi NE St. George, *P 821,* **17 II.**

Psathyrotes ramosissima (Torr.) A. Gray

[Note: Voucher *(Kyhos 58–196)* for a report for this taxon by Ornduff et al. (1963) is *P. annua.*]

AR, Yuma Co., 31 km W county line on Interstate Rte. 10, *S 1220,* **17 II** (3).

CA, Inyo Co., ca 7 mi W Townes Pass, *P 1224,* **17 plus 2 B**; just E Tecopa Pass, *S 1215,* **17 II**; ca 4.8 km N county line on road from Trona to Panamint Valley, *S 1218,* **17 II** (5), **17 II plus 3 B** (1); Death Valley, near Ubehebe Crater, *Powell and Patterson 1611* (TEX), $n = 17$ (unpublished).

CA, Riverside Co., ca 9.5 km E Mecca, *S 1211,* **17 II** (3); ca 16 km E Mecca, *S 1212,* **17 II** (1), **17 II plus 0—3 B** (1), **17 II plus 6 B** (1); Palm Desert, *S 1213,* **17 II** (3); Chiriaco Summit, ca 48 km E Indio, *S 1219,* **17 II** (2), **17 II** or **15 II plus 1 IV** (1).

CA, San Bernardino Co., Rte. 127, just S Ibex Pass, *S 1216,* **17 II** (2); Rte 127, ca 19 km S Ibex Pass, *P 979,* **17 II**; *S 1199,* **17 II plus 0—1 B**; *S 1217,* **17 II** (3).

Psathyrotes pilifera A. Gray

UT, Washington Co., ca 3.2 km E LaVerkin, *S 1202,* **17 II** (4).

Psathyrotes scaposa A. Gray

Chihuahua, 20 mi W Ojinaga, *Powell, Turner, and Sikes 2468* (TEX), $n = 19$ (unpublished).

TX, Brewster Co., Terlingua, *Turner and Ellison 4598* (TEX), $n = 19$ (Turner and Ellison, 1960).

TX, Hudspeth Co., 12 mi W Sierra Blanca, *Powell and Averett 1487* (TEX), $n = 19$ (Powell and Sikes, 1970); 14 mi W Sierra Blanca, *Sikes 459* (SRSC), $n = 19$ (unpublished); 22 mi S Tommy's Town, *Powell 2420* (SRSC), $n = 19$ (unpublished).

TX, Presidio Co., 5.2 mi N Lajitas, *Powell 2391* (SRSC), $n = 19$ (unpublished).

Psathyrotes purpusii Brandeg.

Coahuila, ca 100 km W Saltillo (type locality), *P 715,* **19 II.**

squashes of pollen mother cells that were field-fixed in Carnoy's fluid. Meiosis seemed to be normal in the majority of preparations.

In four colonies of *P. ramosissima* and in one colony of *P. annua,* B-chromosomes were present in some plants. Most colonies for which more than one plant was studied were heterogeneous with respect to presence of B-chromosomes. During meiosis, the B-chromosomes usually behaved as univalents (rarely there was a tendency to associate in pairs), segregated randomly at first anaphase, and divided (usually early) at second anaphase. No laggards were observed; no micronuclei were present in tetrads. Pollen stainability (N = 200, lacto-phenol : cotton blue) ranges from 90 to 98 percent in plants with B-chromosomes and from 72 to 100 percent in plants lacking B-chromosomes. Geographic distribution of plants with B-chromsomes does not suggest a pattern. At present, we can offer no explanation for, nor can we assign any significance to, the occasional presence of B-chromosomes in *Psathyrotes.*

In one plant of *P. ramosissima,* the modal meiotic configuration was 15 II + 1 IV (see Table 1). Whether such translocation heterozygosity has contributed to occurrence of B-chromosomes in *Psathyrotes,* we cannot say.

Species of *Psathyrotes* form two morphologically and geographically natural groups. These groups are also distinct cytologically. The Chihuahuan Desert species have $x = 19$ and the Sonoran Desert-Great Basin species have $x = 17$. Morphologically, the Chihuahuan taxa are less specialized than the Sonoran-Great Basin group. It is reasonable, then, to postulate a dysploid reduction from a Chihuahuan ancestral type to a Sonoran-Great Basin ancestral type.

Of the Chihuahuan pair, *P. purpusii* is more primitive than *P. scaposa,* but each has distinctive, specialized traits indicating a relatively remote divergence from a common ancestor. In the Sonoran-Great Basin trio, *P. annua* seems to represent a northern facies fairly recently derived from *P. ramosissima* or a very recent common ancestor. These two species show occasional, local morphological intergradation where their ranges overlap (see Taxonomic Treatment). *Psathyrotes pilifera* is exceptionally specialized in several morphological traits (e.g., entire leaf margins, multicellular hairs of the herbage, reduced number of florets, capillary pappus, and ribbed achenes). It is closely but obscurely related to the other Sonoran-Great Basin species.

Taxonomic Treatment

Psathyrotes (Nutt.) A. Gray, Smithsonian Contr. Knowl. 5(6):100. 1853. — *Bulbostylis* DC. sect. *Psathyrotus* [sic] Nutt., Proc. Acad. Nat. Sci. Philadelphia 4:22. 1848. Type: *Bulbostylis annua* Nutt.

Tetradymia DC. subg. *Polydemia* Torr., *In* Emory, Notes Mil. Rec. 145. 1848. Type: *Tetradymia ramosissima* Torr.

Psathyrotopsis Rydb., N. Amer. Fl. 34:360. 1927. Type: *Psathyrotes purpusii* Brandeg.

Pseudobartlettia Rydb., N. Amer. Fl. 34:358. 1927. Type: *Psathyrotes scaposa* A. Gray.

Annual or perennial herbs or, rarely, subshrubs. Leaves alternate; petioled; laminar; round-deltoid to suborbicular or reniform; toothed, crenulate, or entire; loosely floccose-tomentose to lanate and/or furfuraceous but not glabrous. Capitulescence monocephalic or a subumbellate or corymbiform cluster of a few heads. Involucres cylindro-turbinate to hemispheric. Phyllaries several (8–24) in 2–3 similar or distinct series. Receptacle flat to convex; smooth to foveolate; glabrous to weakly hispid. Heads discoid; few (9) to several or many (50) flowered. Corollas pale cream to bright yellow, often tipped with red or purple; tube much shorter than the cylindrical throat; lobes 5, short, erect, deltoid, internally papillate, externally stipitate-glandular with bulbous-tipped hairs and often conspicuously to sparsely villous with slender, multicellular hairs. Anthers acute to blunt at apex; weakly to decidedly sagittate at base. Style branches weakly- to shaggy-papillate; rounded-truncate or weakly subulate-appendaged. Achenes cylindrical to obpyramidal; subscabrous to densely hirsute. Pappus of many to numerous, coarse to fine bristles in 1–4 series. Figure 1, a–e.

Key to *Psathyrotes*

1. Leaves cauline, at least somewhat furfuraceous (often tomentose as well); phyllaries clearly of two dissimilar series, at least the inner, chartaceous ones deciduous; Sonoran Desert and Great Basin. . 2.
1. Leaves mostly basal, loosely floccose to lanate but not furfuraceous; phyllaries obscurely of 2–3 similar series, all herbaceous and persistent; Chihuahuan Desert. . . . . 4.

2. Margins of all leaves entire, margins and veins conspicuously ciliate below with long, straight, multicellular hairs; achenes subscabrid, 4–5 mm long. . . . . 3. *P. pilifera.*
2. Margins of at least some leaves toothed, not ciliate with multicellular hairs; achenes densely hirsute, less than 3.5 mm long. . . . . 3.

3. Leaves weakly tomentose and furfuraceous; outer phyllaries erect, apices mostly lance-linear; florets 13–16 (10–20) per head; pappus of 35–50 bristles in one series. . . . . 1. *P. annua.*
3. Leaves velvety lanate and furfuraceous; outer phyllaries apically squarrose to reflexed, apices spatulate to obovate; florets 21–26 (16–32) per head; pappus of 120–140 bristles in 3–4 series. . . . . 2. *P. ramosissima.*

4. Heads borne in corymbiform clusters on branched, scapiform, glandular-puberulent stems; involucres broadly campanulate to hemispheric; phyllaries 4–6 mm long. . . . . 4. *P. scaposa.*
4. Heads borne singly or in subumbellate clusters on rather short, stout, woolly peduncles; involucres narrowly to broadly turbinate; phyllaries 9–10 mm long. . . . . 5. *P. purpusii.*

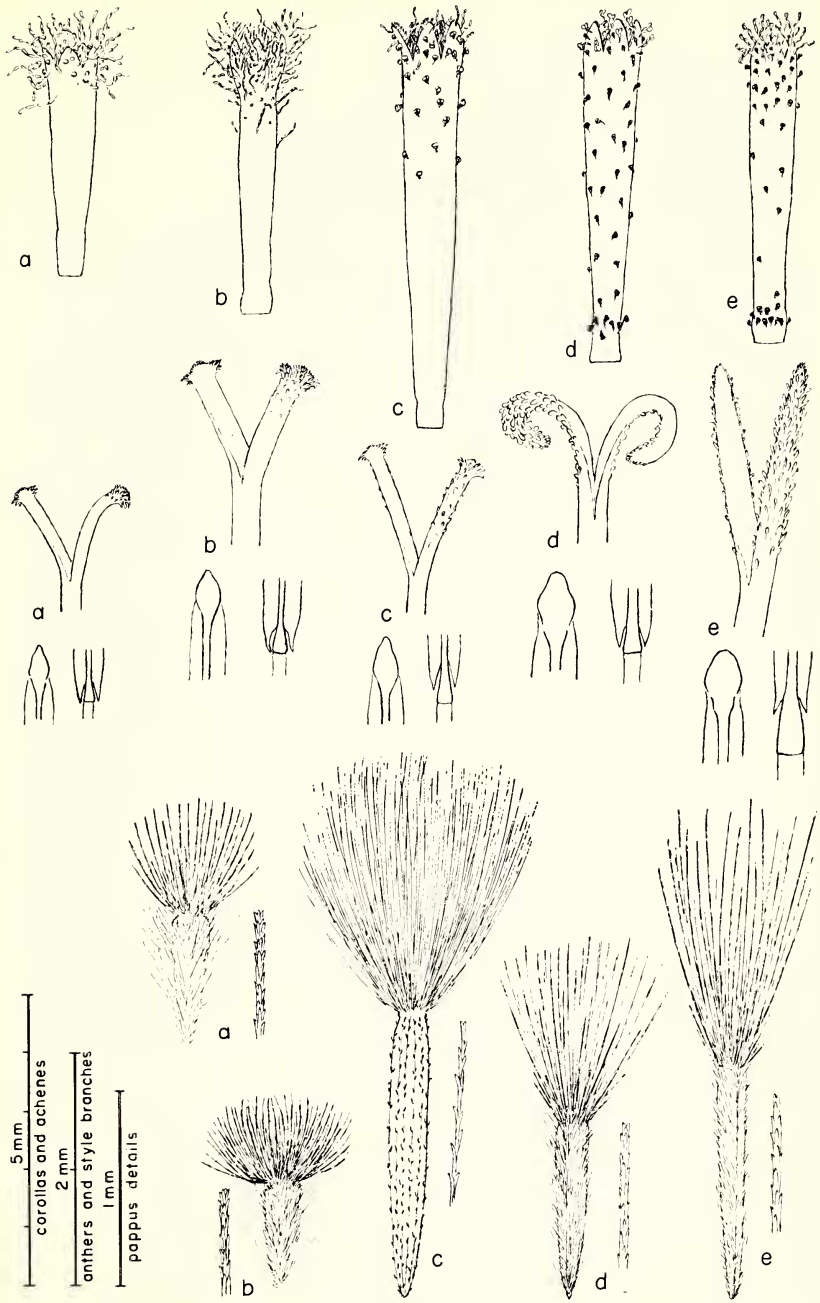

FIG. 1. Sketches of corollas, style branches, anther apices and bases, and achenes of *Psathyrotes*. a. *P. annua* (*Pilz 1185*, UC); b. *P. ramosissima* (*Strother 1220a*, UC); c. *P. pilifera* (*Strother 1202d*, UC); d. *P. scaposa* (*Correll and Flyr 38324*, UC); e. *P. purpusii* (*Pilz 715*, UC).

1. Psathyrotes annua (Nutt.) A. Gray, Smithsonian Contr. Knowl. 5(6):100. 1853.—*Bulbostylis annua* Nutt., Proc. Acad. Nat. Sci. Philadelphia 4:22. 1848. Type: The actual locality cannot be determined with confidence (see McKelvey, 1955; Reveal and Spevak, 1967). "Rocky Mts., near Santa Fe." (protologue and label at GH), "Mts. of U. Calif." (label on holotype at K), no date, *Gambel s. n.*

Freely branched, compact annuals (rarely perennials) 6–12 (4–15) cm high, 8–20 (6–40) cm across when flowering. Stems often purplish, furfuraceous and, sometimes, loosely and weakly tomentose. Leaves greenish to gray-green, furfuraceous and with scattered, subsessile to stipitate, swollen glandular hairs (rarely weakly tomentose as well); petioles stoutish, 4–12 (3–35) mm long; blades 8–15 (4–18) mm long, 9–20 (6–24) mm wide (notably smaller distally), rounded-deltoid to subreniform, usually cuneate, distally weakly to saliently 5–7 (3–9) toothed (rarely a few leaves entire). Heads borne singly on axillary or supra-axillary peduncles 5–15 (1–28) mm long (consecutively shorter distally). Involucres narrowly turbinate. Outer phyllaries 5 (rarely 6), 4–5 (8) mm long, erect, herbaceous, furfuraceous and with minute, subsessile glandular hairs, weakly persistent or deciduous; inner phyllaries mostly 8 or 13, 5–7 (9) mm long, chartaceous basally, distally herbaceous and similar to the outer ones, deciduous. Receptacle foveolate; hispid. Florets 13–16 (10–21) per head. Corollas light yellow, sometimes turning reddish to purplish distally; tube ca 0.5 mm long; throat ca 3 mm long; lobes ca 0.8 mm long, erect, elongate-triangular, papillate within, externally villous and with bulbous-tipped, glandular hairs. Anthers ca 2 mm long; apices triangular-lanceolate; bases sagittate. Style branches rather slender, ca 0.8 mm long; rounded-truncate, papillate. Achenes ca 2.5 (2–3) mm long; narrowly obpyramidal; densely hirsute with tawny to rufous hairs 0.5–1.0 mm long. Pappus of 35–50 coarse, tawny to rufous, subequal bristles 2–3 (1–4) mm long in 1 series. Figure 1,a.

Distribution (fig. 2): SW Idaho (Canon Co.), NW Nevada south to W Mojave Desert (Red Rock Canyon, Lucerne Valley, Twenty-nine Palms) east to W Utah (Tooele, Juab, and Washington counties) and NW Arizona (Mohave Co.). Locally common, mostly on alkaline soils in washes and playas between 800 and 2000 m, exceptionally to 450 m, in association with Creosote Bush Scrub, Shadscale Scrub, or Alkali Sink vegetation. Mid May to mid October.

Plants of *P. annua* and *P. ramosissima* are rather similar in gross morphological aspect and members of each species have been misidentified as the other many times. These misidentifications have doubtless contributed to erroneous geographic statements and to inaccurate morphological descriptions in regional and local floras. Geographic distributions of these species interdigitate and overlap in a few places (fig. 2). We have not found the two actually growing together, however, prob-

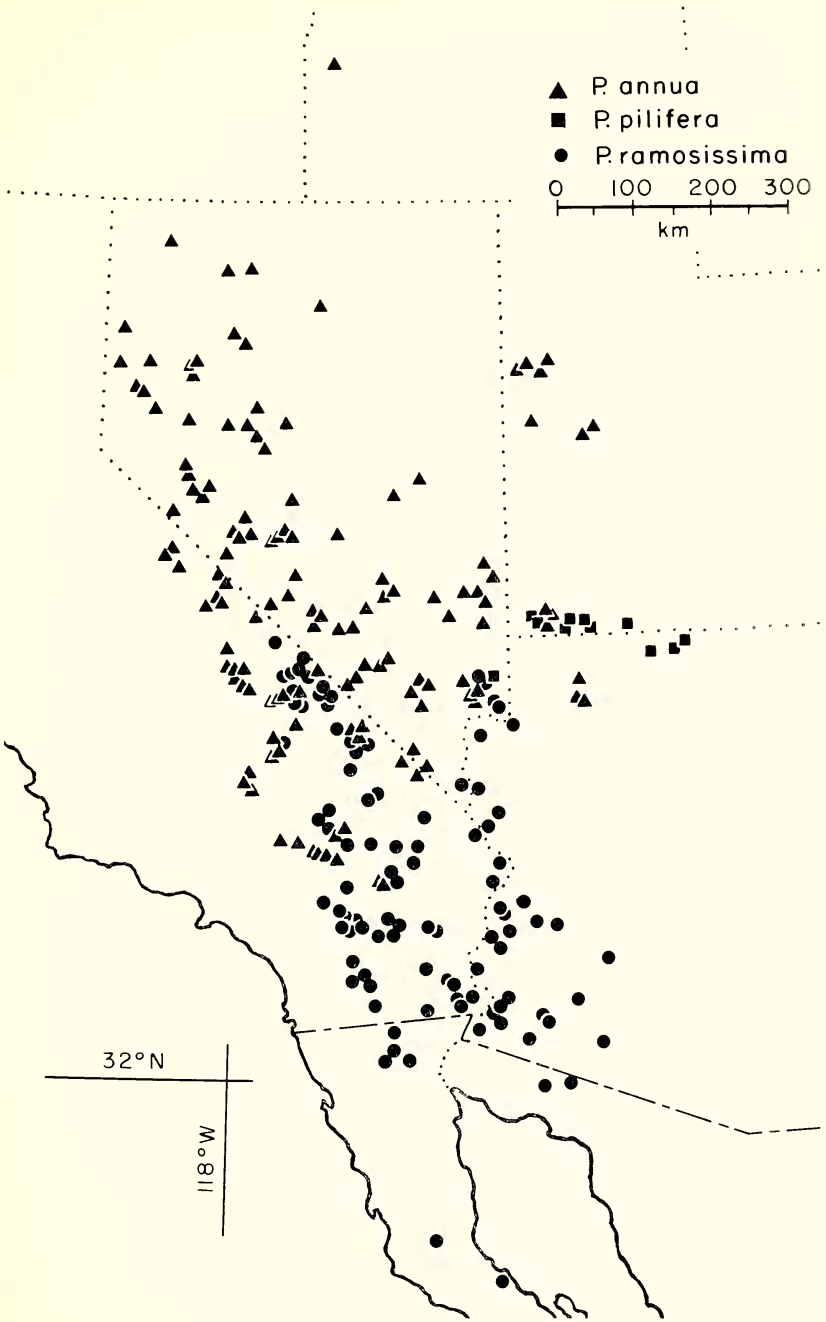

FIG. 2. Distributions of *Psathyrotes*.

ably because *P. annua* generally grows at higher elevations than *P. ramosissima*. But, in some areas of sympatry, plants of *P. annua* vary toward *P. ramosissima*, e.g., *P. A. Munz 14798* (CAS, GH, MO, POM), CA, Inyo Co., Panamint Mts. Wildrose Canyon, 2500 ft.; *Jack Reveal 47a* (UTC), CA, Inyo Co., Eureka Valley, sand dunes, 4800 ft.; *G. T. Robbins 3487* (JEPS), CA, Inyo Co., McLain Park, 8.8 mi S Shoshone, 1400 ft.; and *E. C. Twisselmann 4812* (CAS), CA, San Bernardino Co., Salt Wells Canyon, 1600 ft. These intermediates may be introgressants or they may be products of local selection pressures.

2. Psathyrotes ramosissima (Torr.) A. Gray, Proc. Amer. Acad. Arts 7:363. 1868. — *Tetradymia ramosissima* Torr., *In* Emory, Notes Mil. Rec. 145. 1848. Type: Arizona, southern Yuma Co., "Valley of Gila" (on holotype, NY!), "Hills bordering the Gila" (protologue), 18 Nov 1846, *Emory s. n.*

Freely and intricately branched, compact annuals or short-lived, often suffruticose, perennials 8–15 (3–30) cm high and 10–25 (5–40) cm across when flowering. Young stems lanate; older stems glabrate, shining. Leaves tawny to grayish green; lanate and furfuraceous, distinctly velvety; petioles stoutish, 7–20 (5–35) mm long, sometimes slightly purplish; blades 10–20 (8–25) mm long, 14–22 (8–30) mm wide (smaller distally), rounded-deltoid to subreniform or suborbicular, usually cuneate, distally 5–8 (3–10) toothed, the teeth low, rounded to obtuse-pointed. Heads borne singly on axillary or supra-axillary peduncles 5–15 (3–50) mm long (consecutively shorter distally). Involucres broadly turbinate to campanulate. Outer phyllaries 5 (rarely 6), 5–6 (4–10) mm long, spatulate or dilated at tip and spreading to squarrose or reflexed apically, herbaceous, furfuraceous and lanate and with minute, subsessile, glandular hairs, persistent, somewhat indurate, and strongly reflexed in fruit; inner phyllaries 12–15 (10–18), 6 (5–7) mm long, lanceolate, chartaceous basally, distally herbaceous and similar to the outer ones, deciduous. Receptacle foveolate; hispid. Florets 21–26 (16–32) per head. Corollas light or pale yellow, sometimes turning reddish or purplish distally; tube ca 0.5 mm long; throat ca 3.5 mm long; lobes ca 0.8 mm long, erect, triangular-lanceolate, papillate within, externally villous and with bulbous-tipped, glandular hairs. Anthers ca 2.5 mm long; apices triangular-lanceolate; bases sagittate. Style branches rather stout, ca 1 mm long; rounded-truncate, papillate. Achenes 2–3 (1.5–3.5) mm long; obpyramidal; densely hirsute with tawny to rufous hairs 1–2 mm long. Pappus of 120–140 tawny to rufous, subequal bristles 3–4 mm long in 2–4 series. Figure 1,b.

Distribution (fig. 2): Death Valley region, Inyo Co., California, south through Mojave and Colorado deserts to vicinity of Bahia de San Luis Gonzaga, Baja California, east to Clark Co., Nevada, and the Colorado and Gila rivers in Arizona (Maricopa, Mohave, Pima, and Yuma

counties), and in NW Sonora. Locally common, mostly on sandy soils, often among dunes, sometimes on desert pavement, usually below 600 m, occasionally to 900 m, in association with Creosote Bush Scrub and desert dune vegetation. Mostly mid March to mid May, occasional throughout the year.

Errors on labels and morphological similarity between *P. annua* and *P. ramosissima* have contributed to inaccurate morphological and geographic circumscriptions for *P. ramosissima*. An apparent repeated source of error in reports of distribution of *P. ramosissima* is *Mrs. E. F. Shore 71* (NY), presumably collected near or at Reno, Nevada, in summer 1939. The nearest documented locality for *P. ramosissima* is more than 300 km southeast of Reno. Such a disjunction seems unlikely, and since the intervening area has been reasonably well collected, we believe that the locality given for *Shore 71* is an error.

Erroneous reports of *P. ramosissima* from Utah derive from two sources: misidentification of plants of *P. annua* [e.g., *M. E. Jones s. n.*, in 1896 (POM, US), Fish Springs; and *J. Langenheim 3824* (UC), Millard Co.] and an erroneous locality (St. George) associated with *E. Palmer 266*, in 1877 (NY, UC). Palmer was based in or at St. George in 1877 but he made several excursions including one to St. Thomas, Nevada, in April (McVaugh, 1956). His *"266"* was probably collected then.

3. Psathyrotes pilifera A. Gray, Proc. Amer. Acad. Arts 19:50. 1880. Type: Utah, Kane Co., "near Kanab", *Mrs. A. P. Thompson s. n.*, no date. Lectotype: GH! (Strother, Madroño 22:280. 1974).

Compact, freely branched annuals 6–15 cm high, 6–30 cm across when flowering. Stems tawny; glandular-pubescent and sparsely furfuraceous to subglabrous, sometimes with a few long, straight hairs. Leaves bluish green; sparsely furfuraceous, conspicuously ciliate on margins and veins below with straight, multicellular hairs 5–6 mm long; petioles 8–15 (5–18) mm long; blades 7–14 mm long, 6–14 mm wide (smaller distally), rhombic-rounded, cuneate, acute, entire. Heads borne singly from axils on peduncles 8–15 (4–20) mm long (consecutively shorter distally). Involucres narrowly cylindrical. Outer phyllaries 5, 6–9 mm long, narrowly lanceolate, erect, herbaceous, glandular-puberulent and usually with several conspicuous, straight, multicellular hairs ca 5 mm long, weakly persistent in fruit; inner phyllaries usually 8, 7–9 mm long, lanceolate-linear, mostly chartaceous but for the herbaceous tips, deciduous. Receptacle not pitted; glabrous. Florets 9–14 per head. Corollas pale yellow, sometimes tipped with reddish purple, very slender, cylindrical; tube ca 1 mm long; throat ca 6 mm long; lobes ca 0.8 mm long, erect, triangular, weakly glandular-pubescent with bulbous-tipped hairs and very sparsely villous externally. Anthers ca 3.5 mm long; apices triangular-lanceolate; bases sagittate. Style branches slender, ca 1.5 mm

long; rounded-truncate, papillate. Achenes 4–5 mm long; narrowly cylindrical to weakly fusiform; weakly ribbed; closely subscabrid to subglabrate. Pappus of ca 150 whitish, fine barbellulate bristles ca 5 mm long in 2–4 series and basally connate. Figure 1,c.

Distribution (fig. 2): Restricted to the Dixie-Corridor area in SW Utah (Kane and Washington counties) and adjacent Arizona (Coconino Co.) and Nevada (Clark Co.). Locally common and conspicuous on heavy, often reddish, alkaline soils between 500 and 1400 m in association with ecotones of Creosote Bush Scrub, Pinyon-Juniper, Blackbrush, and Shadscale vegetations (see Cronquist et al., 1972). Sporadic, apparently depending on timing of rains, late June to early October.

We have seen one collection of *P. pilifera* misidentified as *P. annua: Ripley and Barneby 6370* (CAS, NY), NV, Clark Co., 1 mi W Glendale, 19 Jun 1944.

4. Psathyrotes scaposa A. Gray, Smithsonian Contr. Knowl. 5(6):100. 1853. — *Pseudobartlettia scaposa* (A. Gray) Rydb., N. Amer. Fl. 34: 358. 1927. Type: Labels and protologue indicate "Stony hills above El Paso", May 1851, *C. Wright "1416"*. The actual type locality is probably considerably southeast of El Paso, Texas, but it cannot be determined with certainty. Holotype: GH!; isotypes: GH!, MO!, NY!, PH!

Short-lived perennials (often flowering the first year and behaving as annuals) 8–30 (40) cm high when flowering. Caudices few-branched below; current aerial stems little to freely branched above. Leaves mostly basal; greenish to grayish; loosely floccose-tomentose; petioles 2–3 (1–5) cm long; blades 3–4 (1–6) cm long, 2–3 (1–4) cm wide, broadly lanceolate to ovate or rounded-deltoid, cuneate, margins crenate to subentire. Heads borne in tight to loose corymbiform clusters, terminating the branches of the glandular-puberulent, scapiform stems. Involucres broadly campanulate to hemispherical. Phyllaries 16–20 (8–21); obscurely in 2–3 similar series; 4–6 mm long; narrowly lanceolate; apically ciliate; dorsally glandular-puberulent; persistent and strongly reflexed in fruit. Receptacle not pitted; glabrous. Florets 25–40 (16–50) per head. Corollas bright yellow to almost white; tube ca 0.5 mm long, constricted; throat cylindrical, ca 4 mm long; lobes ca 0.5 mm long, erect to spreading, short-villous; throat and lobes bearing bulbous-tipped, glandular hairs. Anthers ca 3 mm long; apices ovate, blunt; bases weakly sagittate. Style branches ca 2.5 mm long; often curled; shaggy-papillate; rounded or conical at tip. Achenes 2.5–3.5 mm long; very narrowly obconical; sparsely hirsute with tawny hairs ca 0.5 mm long. Pappus of ca 80 tawny to rufous, unequal, coarse, smooth, blunt bristles 1–3 mm long in 2–3 series. Figure 1,d.

Distribution (fig. 3): W Texas (Brewster, Hudspeth, Jeff Davis, and Presidio counties) and adjacent Chihuahua. Locally common on gypseous, calcareous clays or on limestone outcrops between 750 and

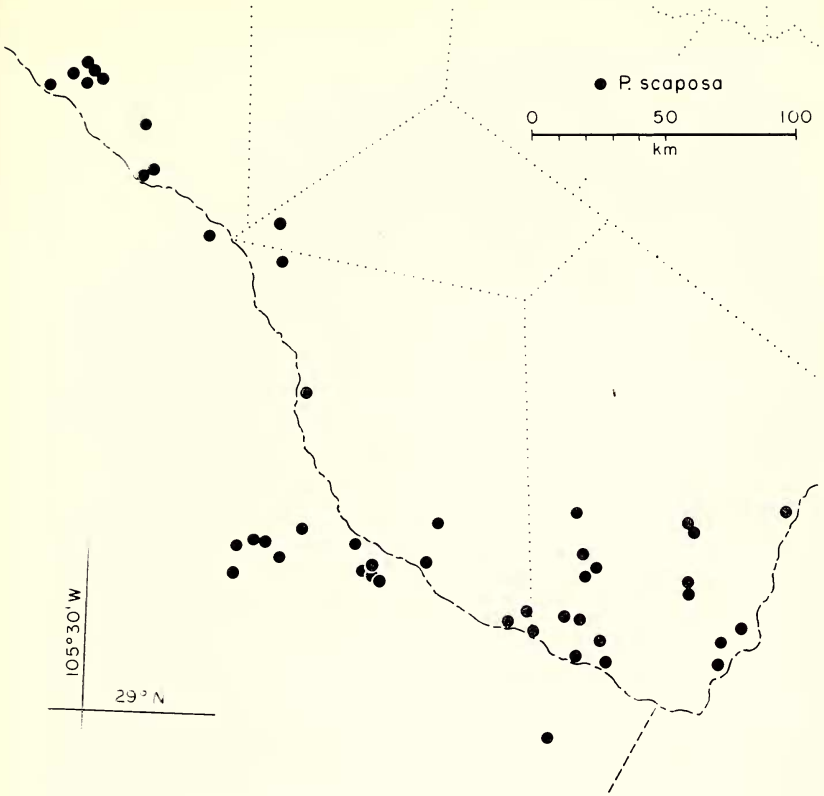

FIG. 3. Distribution of *Psathyrotes scaposa*.

1250 m in association with Creosote Bush Scrub vegetation. Bi-seasonal, late March to early May and in October, sporadic through summer.

Style branches have long been heavily weighted as a source of characters in classification of Compositae and the generally conservative nature of style branches indicates that such weighting is justified. The contrast then between the smooth, rounded-truncate style branches of the Sonoran Desert-Great Basin members of *Psathyrotes* and the shaggy-papillate, conically rounded style branches of *P. scaposa* and *P. purpusii* in the Chihuahuan Desert is unusual. This heterogeneity within *Psathyrotes* illustrates that expression of this character can vary even among closely related species and may serve as a caution against excessive reliance on style branch characters.

5. PSATHYROTES PURPUSII Brandeg., Univ. Calif. Publ. Bot. 4:193. 1911. — *Psathyrotopsis purpusii* (Brandeg.) Rydb., N. Amer. Fl. 34:360. 1927. Type: Coahuila, ca 100 km W Saltillo, "foot of Sombreritito, near Marte" (a railroad station), Oct 1910, *C. A. Purpus 7463*. Holotype: UC!; isotypes: GH!, MO!

Low perennial herbs from branched caudices. Stems of current season densely lanate. Leaves clustered at the tips of the branched caudex; loosely tomentose, gray-green above, densely lanate, canescent below; petioles 8–20 mm long; blades 12–28 mm long, 10–20 (30) mm wide, ovate to rounded-deltoid or subreniform, truncate to cuneate, margins distinctly and finely crenulate. Heads borne singly or in subumbellate clusters of 2–6 from upper axils on stout, woolly peduncles 8–20 mm long. Involucres narrowly to broadly turbinate. Phyllaries 15–21; obscurely in 2–3 series; 9–10 mm long; subequal; linear; woolly dorsally and ciliate apically; persistent and strongly reflexed in fruit; the innermost ones with narrow hyaline margins. Receptacle not pitted; glabrous. Florets 35–40 (20–50) per head. Corollas at first creamy yellow, becoming purplish apically; tube ca 0.5 mm long; throat ca 5 mm long; lobes ca 0.8 mm long, deltoid, erect to spreading, internally papillate, externally short-villous and with bulbous-tipped, glandular hairs. Anthers ca 3.5 mm long; apices ovate, blunt; bases weakly sagittate. Style branches ca 2 mm long; often curled; shaggy-papillate; rounded or conical at tip. Achenes 3.5–4.5 mm long; narrowly cylindrical; obscurely striate; sparsely hirsute with tawny hairs to 0.5 mm long. Pappus of ca 80 smooth, slender, unequal bristles 1–4 mm long in 2–3 series. Figure 1,e.

Distribution: Known only from the type locality where we found it growing at ca 1200 m in light, sandy soil at the foot of talus (*Pilz 715*, 26 Jul 1971). July and October.

Excluded Names

Psathyrotes (Nutt.) A. Gray sect. *Peucephyllum* (A. Gray) A. Gray, Proc. Amer. Acad. Arts 9:206. 1874. ≡ Peucephyllum A. Gray, Bot. Mex. Bound. 74. 1859. [Type: Peucephyllum schottii A. Gray]

Psathyrotes incisa A. Gray, Mem. Amer. Acad. Arts, ser. 2. 5:322. 1854. [Type: California, "desert near the Rio Colorado" (protologue), "Desert west of Colorado" (label on holotype, GH!), Feb 1852, *Geo. Thurber s. n.*] ≡ Trichoptilium incisum (A. Gray) A. Gray, Bot. Mex. Bound. 97. 1859.

Psathyrotes schottii (A. Gray) A. Gray, Proc. Amer. Acad. Arts 9:206. 1874. ≡ Peucephyllum schottii A. Gray, Bot. Mex. Bound. 74. 1859. [Type: Sonora, "Diluvial banks of the Colorado" (protologue), 3 Feb 1855, *A. C. V. Schott 45*. Holotype: GH! isotype: F!]

List of Exsiccata

Nearly 1000 herbarium specimens representing about 520 gatherings were examined during the course of this study (see list of herbaria in Acknowledgments). These, together with our field observations, are the basis of our descriptions, phenological statements, and distribution maps.

A list of *Psathyrotes* collections, arranged alphabetically by collectors' last names and chronologically by collection numbers or dates (for unnumbered collections) for each collector, is on file in UC and has been distributed to herbaria cited in Acknowledgments. Additional copies of the list are available from Strøther.

Acknowledgments

We are grateful to curators and staffs of the following herbaria for loans of specimens and/or other courtesies: A, ASU, CAS, COLO, DS, F, GH, JEPS, MO, NY, OKL, OKLA, ORE, PH, POM, RM, RSA, SMU, TEX, UBC, UC, US, UTC, WIS, WS, and WTU. We are especially grateful to A. J. Hill, A. M. Powell, and S. Sikes for allowing us to include here their previously unpublished chromosome counts. This research was supported in part by NSF grants GB 7995 and GB 36647.

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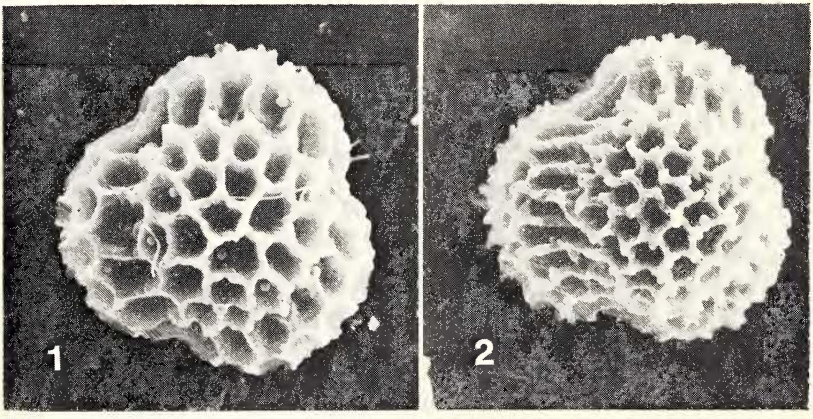
Announcement of Meeting.—The California Botanical Society will hold its second graduate student meeting 12–13 April 1975 at University of California, Davis. The meeting will take the form of a series of papers contributed by students. Members and non-members of the Society are invited to attend. For registration forms or other information contact Leslie D. Gottlieb, Department of Genetics, University of California, Davis 95616.

Sphaerocarpos michelii Bell.: A New Liverwort for California.—A population of *Sphaerocarpos michelii* was recently discovered growing on damp loamy soil along the bank of an ephemeral creek on the drier soil of a marshy portion of the creek bed where the creek crosses California Highway 91 about 18.2 km west of the junction of this road with California Highway 139 in Modoc County (*Doyle 1974,* UC). The plants were fairly abundant, but few sporophytes were present, and grew in association with three species of *Riccia.*

The female plants of *S. michelii* from Modoc County have small, terete bottles surrounding unfertilized archegonia and pyriform ones surrounding mature sporophytes and closely resemble female plants of *S. cristatus* Howe. *Sphaerocarpos michelii* grows intermingled with *S. texanus* Aust. in the United States (Bryologist 51:168–169. 1948). The female bottles of *S. texanus* are generally tubular to fusiform-clavate. Because of environmental plasticity of this character, however, details of spore markings and spore tetrad size are the best means to species identification. Spores of *S. cristatus* are separate at maturity, while those of *S. michelii* and *S. texanus* remain adherent as tetrads. In contrast to *S. texanus,* the spore tetrad of *S. michelii* is smaller, the walls of the reticulations are lower, and the intersections of the walls are elevated to form blunt spines (figs. 1–2).—William T. Doyle, Biology, University of California, Santa Cruz 95064.



Figs. 1–2. Scanning electron micrographs of spore tetrads of *Sphaerocarpos* spp. 1. *S. texanus* (California: Monterey Co., *Doyle 1973,* UC), end view, ca × 361. 2. *S. michelii* (California: Modoc Co., *Doyle 1974,* UC) end view, ca × 472.